

Structure and Function of the Alimentary Tract of *Batillaria zonalis* and *Cerithidea californica*, Style-Bearing Mesogastropods

BY

ANDREW L. DRISCOLL¹

Pacific Marine Station, Dillon Beach, California 94929

(8 Text figures)

INTRODUCTION

THE FAMILY Potamididae is represented on the California coast of North America by two genera, each represented by a single species: *Batillaria zonalis* Bruguière, 1792, and *Cerithidea californica* Haldeman, 1840. The use of the name *Batillaria zonalis* is in accordance with the conclusions of HANNA (1966). References in the literature concerning these two species are primarily taxonomic with the exception of two papers on the gross morphology of *C. californica* by BRIGHT (1958, 1960).

This study describes the structure and function of the alimentary tracts of *Batillaria zonalis* and *Cerithidea californica* with particular emphasis on the stomach and style sac region. Both species were found to be generally similar to other style-bearing mesogastropods in that they have little or no development of glandular tissue in the esophageal region and a functional style is present in the stomach. The stomachs of both species are specialized to transport and digest a continuous supply of detritus by means of complex ridges, grooves, and ciliary currents. *Cerithidea californica* appears more highly specialized for feeding on fine, highly organic detrital material than *B. zonalis* due to slightly more complex stomach morphology. A possible correlation is postulated between the length of the crystalline style, relative to shell height, and the percentage of organic matter in the detritus ingested.

METHODS AND MATERIALS

Specimens of *Batillaria zonalis*, ranging in size from 25 to 46 mm, were collected along the shores of Tomales Bay (Figure 1, B. z.), while those of *Cerithidea californica* (Figure 1, C. c.), ranging in length from 25 to 32 mm, were collected in Drakes Estero, California. All the collecting stations were sampled from 7 to 10 times between March, 1966 and July, 1967.

Specimens used for histological examination were removed from their shells and relaxed in 1% propylene phenoxylol in sea water before being killed and fixed in Bouin's fixative. Paraffin sections, 10 μ and 12 μ thick, were stained with Alcian Blue, Mayer's Haemalum, and counterstained with Eosin, using standard techniques found in HUMASON, 1962.

Both living and preserved specimens were dissected. Living specimens were dissected immediately after collection, others after being starved for 3 to 4 weeks in the laboratory. Ciliary currents were determined with the aid of carmine and graphite particles suspended in sea water.

Sediment samples from each collecting station were taken, dried and weighed. They were then resuspended in water and analyzed by wet sieving, using 5 sieves ranging from 1 mm to 0.065 mm mesh. The 5 fractions were then dried and weighed separately to obtain the particle size distribution of the substratum.

All laboratory work was performed at the Pacific Marine Station, Dillon Beach, California.

¹ Present address: Marine Environmental Center, Poulsbo, Washington 98370

HABITAT

Batillaria zonalis is native to Japan and according to BARRETT (1963) may have been introduced to Tomales Bay as early as 1928 when the first experimental sets of *Crassostrea gigas* (Thunberg, 1793) were planted in the bay. However, the first observation of this species along the coast of California was reported in 1930 (BONNOT, 1935a). *Crassostrea gigas* was also introduced to Drakes Estero and Bodega Bay in 1932 (BONNOT, 1935b), but no specimens of *B. zonalis* were observed at either locality.

KEEN (1963) stated that the range of *Cerithidea californica* extends from Lower California northward to Bo-

linas, California. In this study, *C. californica* was collected further to the north in Drakes Estero, California. MACDONALD (1969) observed *C. californica* in Tomales Bay, but did not collect any.

Both *Batillaria zonalis* and *Cerithidea californica* inhabit intertidal brackish mudflats and marshes. *Batillaria zonalis* was collected on the Walker Creek Delta (Figure 1, B. z. - 1) and next to Willow Point at the head of Tomales Bay (Figure 1, B. z. - 2). At both localities the animals experienced wide fluctuations in temperature and salinity. On the Walker Creek Delta animals were found in pools of 2 to 5 cm depths, in tidal channels, and on detritus-covered rocks and gravel. Occasionally the substratum was dry where the animals were found. A sediment analysis of the Delta surface mud showed 50% of the particles were between 0.065 and 0.25 mm in diameter and 50% were less than 0.065 mm in diameter. Less than 50% of the surface sediment was organic in nature. During cold weather the snails were found 1 to 2 cm beneath the surface. The length of *B. zonalis* rarely exceeded 25 mm at this station. Young snails with a length of 2 mm were first noted in May.

The Willow Point collecting area was an abandoned man-made ditch which was about 5 to 7 m wide and at least 0.5 m deep. The ditch water was stagnant except for slight tidal exchange and the sediment was similar to that on the Walker Creek Delta. In contrast to the specimens collected at the Walker Creek Delta, the animals in this area were generally over 40 mm long, with a maximum length of 46 mm noted.

Cerithidea californica was collected at the north end of Schooner Bay in Drakes Estero (Figure 1, C. c. - 1) in a marsh area and in small man-made pools next to the Johnson Oyster Company (Figure 1, C. c. - 2). Both localities experienced fluctuations in temperature and salinity. At the Schooner Bay locality the animals were found along tidal channels which were 2 to 4 cm deep, and in the marsh. Some areas of the channels were quite densely populated by the snails. Snails were never found on a dry substratum. A sediment analysis of the surface mud showed 5% of the particles were between 0.065 and 0.25 mm in diameter, and 95% were smaller than 0.065 mm. More than 80% of the surface sediment was organic in nature. During cold weather the animals were found just beneath the surface. The length of *C. californica* rarely exceeded 25 mm here or at the second locality. Developing larvae still within their protective egg cases were collected in June.

At the Johnson Oyster Company *Cerithidea californica* was collected from unused man-made algae culture pools. The pools were dug into the marsh just above mean high tide so there was little direct exchange with the estero

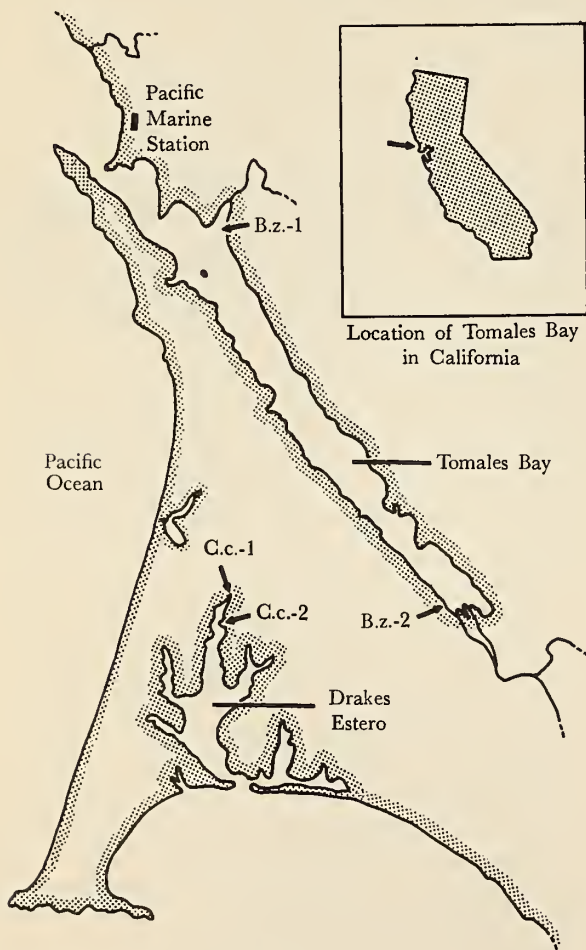


Figure 1

Map of Tomales Bay and Drakes Estero showing collecting stations: B.z. - *Batillaria zonalis*; 1 - Walker Creek Delta; 2 - Willow Point; C.c. - *Cerithidea californica*; 1 - Schooner Bay; 2 - Johnson Oyster Company

water. The pools were 3 to 4 m in diameter and had 5 to 10 cm deep water in them. The pools were carpeted with living and dead snails and the sediment was similar to that found at Schooner Bay.

In no instance was either *Batillaria zonalis* or *Cerithidea californica* found coexisting in the localities sampled. MACDONALD (1969) stated that although *C. californica* was present in Tomales Bay, it was not found in the samples where *B. zonalis* was collected.

MORPHOLOGY

The alimentary tract of *Batillaria zonalis* (Figure 2a) and of *Cerithidea californica* (Figure 2b) can be conveniently divided into 5 regions: (1) the buccal complex including radula and mucous glands; (2) the esophagus; (3) the stomach and style sac; (4) the digestive diverticula; and (5) the intestine.

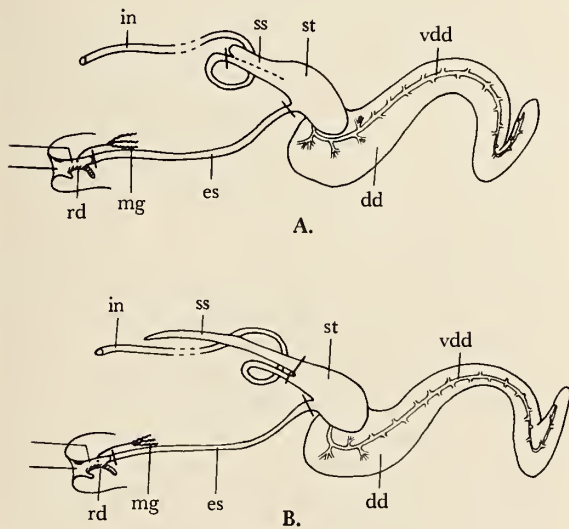


Figure 2

A. Diagram of the alimentary tract of *Batillaria zonalis*.

B. Diagram of the alimentary tract of *Cerithidea californica*.

The boundaries of the major regions of the alimentary tract are marked with solid lines.

bc - buccal cavity; dd - digestive diverticula; es - esophagus; in - intestine; mg - mucous glands; mo - mouth; rd - radula; ss - style sac; st - stomach; vdd - ventral duct of the digestive diverticula

Buccal Complex:

In *Batillaria zonalis* (Figure 3) the mouth (mo) opens into the buccal cavity (bc), the anterior limit being the

pair of horny jaws (hj) on the anterior dorsal surface and the posterior limit being the point at which the radula sac (rs) is separated from the lumen of the gut (GRAHAM, 1939). Posterior to the jaws, the dorsal surface of the buccal lining, consisting mainly of columnar epithelium, becomes folded longitudinally (Figure 4, lf). The pair of dorsal grooves (dg) created by the dorsal longitudinal folds is heavily ciliated and conspicuous mucous cells are

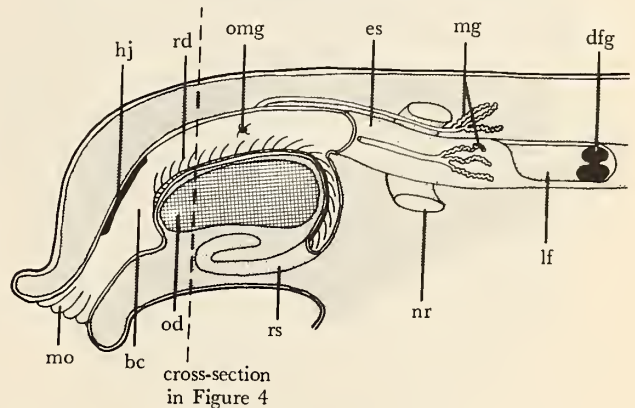


Figure 3

Diagrammatic longitudinal section of the buccal region of *Batillaria zonalis* showing the inside of the buccal cavity and a portion of the inside of the esophagus.

bc - buccal cavity; dfg - dorsal food groove; es - esophagus; hj - horny jaws; lf - lateral folds; mg - mucous glands; mo - mouth; nr - nerve ring; od - odontophore; omg - opening of the duct from the mucous glands; rd - radula; rs - radula sac

present in the lining of the grooves. The dorsal folds extend beyond the posterior limit of the buccal cavity forming the beginning of a dorsal food groove. The lateral lining of the buccal cavity is smooth anteriorly and becomes folded posteriorly. The ciliated epithelial layer thickens posteriorly. The floor of the buccal cavity is covered by a thick cuticle with the exception of the extreme edges of the cavity where there are two small ciliated pockets (cp) of unknown function. The entire buccal mass is surrounded by a thick layer of complex musculature.

The radula (Figure 3, rd) is produced in the radular sac (rs) which opens ventrally into the posterior end of the buccal cavity. The number and type of teeth in each row of the radula is taeniglossan with one central tooth, one pair of lateral teeth, and two pairs of marginal teeth (FRETTER & GRAHAM, 1962). The radula extends anteriorly out of the radular sac and is held against the floor of the buccal cavity by a radular membrane. The radula is

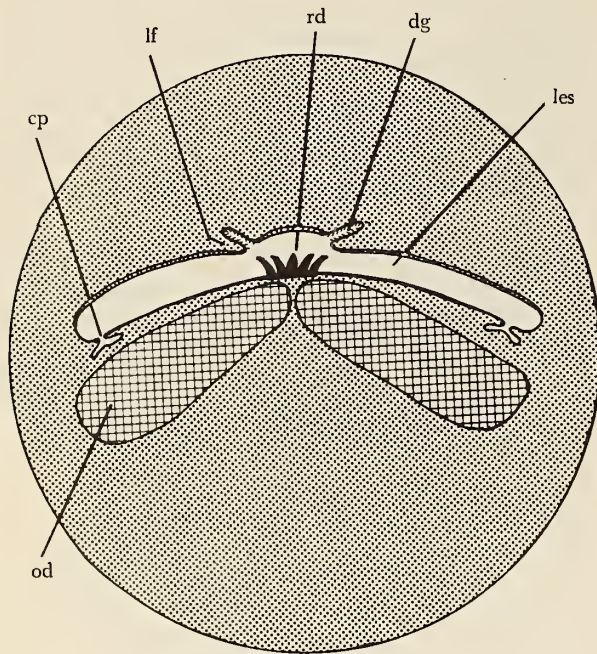


Figure 4

Diagram of a cross section through the middle of the buccal mass of *Batillaria zonalis*.

cp - ciliated pockets; dg - dorsal grooves; les - lumen of the esophagus; lf - longitudinal fold; od - odontophore; rd - radula

supported by the cuticular lining of the buccal cavity and a pair of odontophores (od).

In 8 specimens of *Batillaria zonalis* the shell length ranged from 28 to 45 mm and the radula length ranged from 2.5 to 3 mm and never exceeded twice the length of the buccal cavity. The average ratio of radula length to shell length was 0.11, which is lower than the lowest ratio reported by FRETTER & GRAHAM (1962) of 0.30 for *Nucella lapillus* (Linnaeus, 1758). Fretter and Graham indicated that radula length, as measured by the above ratio, appears related to the substratum type. The radula is long where the substratum is coarse, causing heavy wear, and short where the substratum is soft.

Dorsal to the opening of the radula sac and lateral to the dorsal ciliated grooves, a pair of ducts from the pair of buccal mucous glands (mg) open into the buccal cavity. Each of the buccal mucous glands lying along the dorsal surface of the esophagus (es) is composed of 3 to 4 small convoluted tubules.

The morphology and histology of the buccal complex of *Cerithidea californica*, as described by BRIGHT (1958) is similar to that of *Batillaria zonalis*.

In 5 specimens of *Cerithidea californica* the shell length ranged from 28 to 30 mm and the radula length ranged from 2.5 to 3 mm. The average ratio of radula length to shell length was a low 0.09. A relationship between short radula length and soft substratum seems evident in this species also. The paired buccal mucous glands composed of 3 to 4 small tubules are very similar to those in *Batillaria zonalis*.

Other mesogastropods with similar buccal complex morphology are *Bithynia tentaculata* and *Pomatias elegans*, family Hydrobiidae, and *Melanopsis praemorsa* and *Melania zenganus*, family Melaniidae (GRAHAM, 1939). All possess the beginning of a dorsal food groove as found in *Batillaria zonalis*.

Esophagus:

The esophagus of *Batillaria zonalis* (Figure 3, es) is a tube which begins at the opening of the radula sac and extends to the stomach. As in other style-bearing gastropods, a dorsal food groove (dfg) is formed by 2 lateral folds (lf) which are continuations of the lateral folds in the dorsal wall of the buccal cavity. Posterior to the nerve ring (nr) the lateral folds twist to the left and the groove becomes ventrally located due to torsion. The lateral folds end at a point midway between the radula sac opening and the stomach.

The epithelial lining of the dorsal food groove contains conspicuous mucous cells and is surrounded by a layer of muscle. The ventral esophageal lining is nonciliated and surrounded by a thin muscle layer. Anteriorly, the ventral lining is partially composed of large columnar cells unlike those lining the dorsal food groove. These cells, which appear glandular in nature, form small longitudinal ridges on the ventral wall and on the ventral side of the lateral folds in the esophagus. Posteriorly, the large columnar cells are replaced by typical columnar epithelial cells. The function of the large columnar cells is unknown. GRAHAM (1939) describes similar specialized cells of unknown function occurring in the ventral esophagus of *Rissoa parva*, *Hydrobia* sp., and *Turritella communis*, all style-bearing mesogastropods. The posterior esophagus of *Batillaria zonalis* is thin-walled, ciliated, and folded longitudinally just before entering the stomach.

In *Cerithidea californica* the esophagus has been divided into 3 regions by BRIGHT (1958); a pre-esophagus, a mid-esophagus with a large expanded region, called a "crop," and a post-esophagus. These divisions are based on differences in gross morphology and histology only. GRAHAM (1939) stated that the esophagus of style-bearing gastropods performs the single function of food trans-

port, and since this was also found to be the case in *Cerithidea californica*, divisions will not be stressed in this functional approach.

In contrast to *Batillaria zonalis*, the esophageal food groove of *Cerithidea californica* ends after becoming ventrally located as the whole esophageal lining becomes longitudinally folded. This folded area may be a vestige or a suppression of the glandular pouches of non-style-bearing gastropods (GRAHAM, 1939). The wall of the esophagus becomes spirally ridged just before entering the stomach, unlike the longitudinal folds present in *B. zonalis*. Throughout the esophageal lining in *C. californica* there are conspicuous mucous cells. No large columnar cells were seen as were observed in *B. zonalis*.

Stomach and Style Sac:

In *Batillaria zonalis* the stomach (Figure 5) is the largest organ in the body whorl. The stomach, when opened by a dorsal longitudinal slit, is sac-like with the esophagus entering mid-ventrally (eso), and the intestine opening topographically anteriorly (in). Adjacent posteriorly and topographically to the right of the esophageal opening is the opening to the duct of the digestive diverticula (odd). The adjacent position of these openings is common to many style-bearing mesogastropods such as *Mysorella costigera* (SESHAIYA, 1930), *Hydrobia* sp. and *Bythynia tentaculata* (GRAHAM, 1939). Mid-ventrally, to the right of both openings is a large muscular stomach ridge (lr) extending almost the full length of the stomach proper. The posterior end of the large ridge becomes smaller and thinner (sr), curving to the left and extending anteriorly to the opening to the duct of the digestive diverticula. The lateral groove formed by this stomach ridge channels food material from the esophagus toward the gastric shield. To the right of the anterior half of the stomach ridge lies the gastric shield (gs), a smooth, cuticularized area of the stomach lining. The shield provides a firm surface against which the style rotates. The dorsal wall of the stomach (sa) has many small, closely set ciliated ridges which begin on the right side and extend to the left toward the opening of the intestine. These ridges function as a sorting area for food particles.

The lining of the stomach is composed of columnar epithelium which is ciliated except for the area of the gastric shield and the ventral stomach wall between the gastric shield and the opening to the style sac. Beneath the epithelial lining is a thin, but distinct layer of muscle which plays an important role in moving food through the stomach and the digestive diverticula. The presence of a muscle layer in the stomach wall is similar to what SESHAIYA (1930) found in *Mysorella costigera*, but is in contrast to *Struthiolaria papulosa* which lacks any stomach musculature (MORTON, 1951).

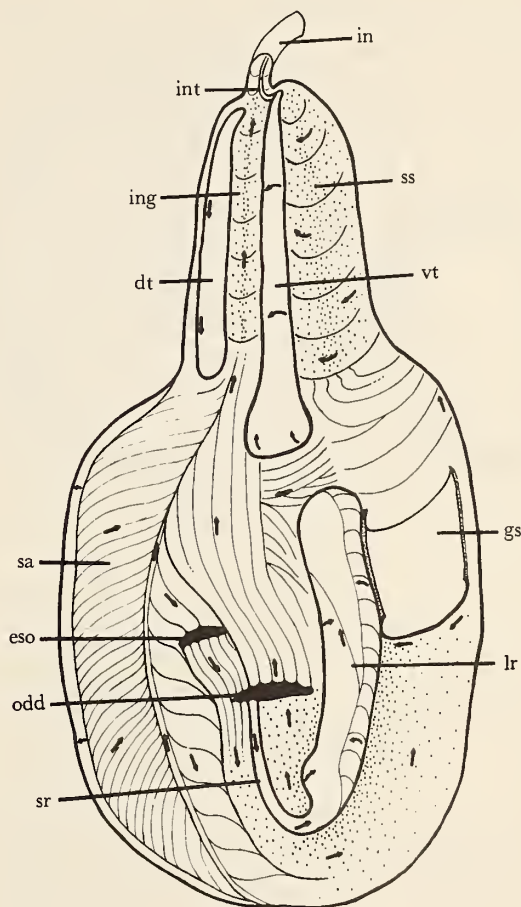


Figure 5

Diagram of the stomach of *Batillaria zonalis*.

The dorsal wall is cut open longitudinally and laid back to the right and left. The arrows represent direction of ciliary beat.

dt - dorsal typhlosole; eso - esophageal opening; gs - gastric shield; in - intestine; ing - intestinal groove; int - intestinal typhlosole; lr - large ridge; odd - opening of the digestive diverticula; sa - sorting area on the dorsal wall; sr - small ridge; ss - style sac; vt - ventral typhlosole

The anterior extension of the stomach proper (Figures 5, 6) contains the ventral (vt) and dorsal typhlosoles (dt), intestinal groove (ing), and the style sac (ss). The ventral typhlosole begins as a muscular bulge at the anterior edge of the stomach proper and narrows as it extends posteriorly to the end of the style sac. This is in contrast to most style-bearing mesogastropods which have a promi-

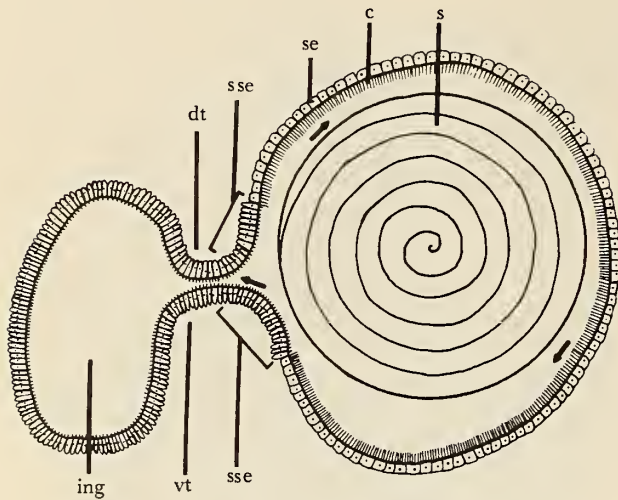


Figure 6

A cross section of the style sac and intestinal groove in *Batillaria zonalis*

c - ciliary lining of the style sac; dt - dorsal typhlosole;
 ing - intestinal groove; s - style; se - style sac epithelium;
 sse - style secreting epithelium; vt - ventral typhlosole

ment ventral typhlosole which begins near the esophageal opening (GRAHAM, 1939). At the posterior end of the style sac the ventral typhlosole continues into the intestine (int). The dorsal typhlosole extends from the stomach proper and terminates at the posterior end of the style sac. The two typhlosoles come into contact with each other and functionally block communication between the style sac on the right side and the intestinal groove on the left side (Figure 6). Only at the anterior end of the style sac is there a sufficient opening for material to move between the style sac and the intestinal groove. The style sac is lined with ciliated cuboidal epithelium (Figure 6, se) except along the sides of the typhlosoles where the surface is composed of tall ciliated columnar epithelium (se) and style-secreting epithelium (sse). The intestinal groove (ing) is lined with ciliated columnar epithelium.

The style sac contains the style (s), which is a tapered hyaline rod. In cross-section the style is a spiral coil of material usually consisting of 3 or 4 layers with the outer layer being thickest. The small posterior end of the style sometimes contains a few food particles from the intestinal groove which are bound into the style material. The style is spongy and dissolves rapidly in sea water or alcohol soon after it is removed from the animal. In 11 specimens the length of the style ranged from 4 to 6 mm.

The ratio of style length to shell height was 0.13.

The stomach of *Cerithidea californica* has been described and figured in general terms by BRIGHT (1958). Bright described the esophageal opening as occurring at the anterior end of the stomach and so figured it. Observations made during this study on 50 specimens, both living and preserved, indicate that the esophagus enters midventrally rather than anteriorly (Figure 2, es; Figure 7, eso).

Within the stomach of *Cerithidea californica* (Figure 7) there is a large midventral stomach ridge (lr) which originates to the right of the opening of the duct of the

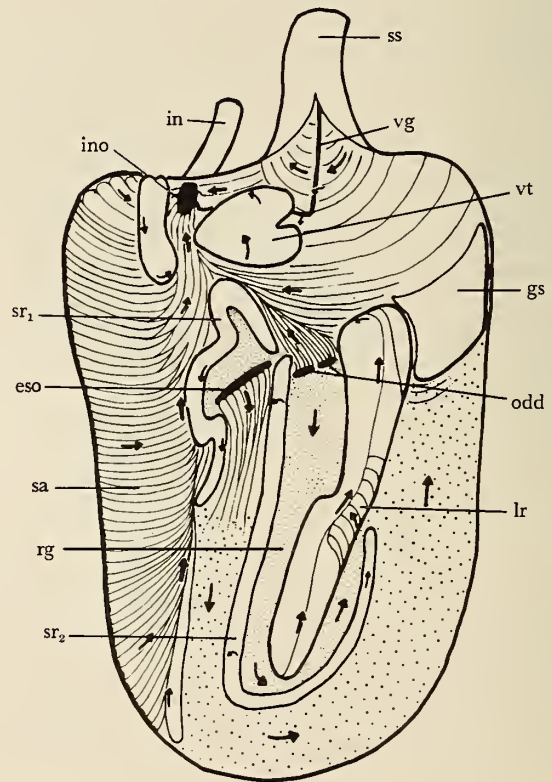


Figure 7

Diagram of the stomach of *Cerithidea californica*.

The dorsal wall is cut open longitudinally and laid back to the right and left. The arrows represent direction of ciliary beat.
 eso - esophageal opening; gs - gastric shield; in - intestine;
 ino - intestinal opening; lr - large ridge; odd - opening to the
 digestive diverticula; rg - recycling groove; sa - sorting area
 on dorsal wall; sr₁ - small ridge -1; sr₂ - small ridge -2;
 ss - style sac; vg - ventral groove in style sac; vt - ventral
 typhlosole

digestive diverticula (odd) and extends posteriorly, ending near the base of the stomach. This is in contrast to the large stomach ridge in *Batillaria zonalis* which curves anteriorly after nearing the base of the stomach.

In addition to the midventral stomach ridge there are two smaller ridges (sr_1 and sr_2) in *Cerithidea californica*. The anterior portion of the first small ridge (sr_1) forms a V with the apex pointed toward the intestinal opening and the angle of the V abutting the esophageal opening. This ridge prevents food entering from the esophagus (eso) from being carried by ciliary currents directly into

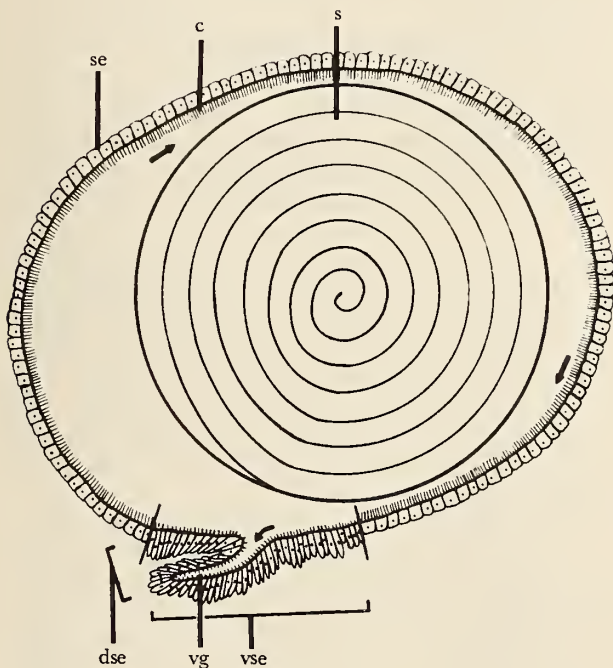


Figure 8

Cross section of the style sac in *Cerithidea californica*.

c - ciliary lining of style sac; dse - dorsal style secreting epithelium; s - style; se - style sac epithelium; vg - ventral groove; vse - ventral style secreting epithelium

the intestine. The second small ridge (sr_2) extends from a point between the esophageal opening and the opening to the duct of the digestive diverticula posteriorly around the base of the large ridge and then anteriorly toward the gastric shield (gs), ending about the middle of the large ridge. SESHAIYA (1930) described a single long V-shaped ridge in *Mysorella costigera* which functions in the same manner as the two small ridges in *C. californica*.

The stomach lining in *Cerithidea californica* is composed of columnar epithelium which is ciliated except

for the areas of the gastric shield and the ventral wall between the gastric shield and the opening of the style sac.

The anterior extension of the stomach in *Cerithidea californica* consists of a style sac (Figure 7, ss; Figure 8). The style sac opening is next to the opening of the intestine (ino) and communicates with it for a distance of less than 1 mm. Posteriorly the style sac and intestine are completely separated. There is a prominent longitudinal ventral groove (vg) in the style sac which was not described by BRIGHT (1958). The groove is bounded on both sides by several rows of tall, ciliated columnar epithelial cells (dse and vse) and mucous cells. These cells are similar to those found on the edge of the typhlosoles in the style sac of *Batillaria zonalis* and their function is also similar. There is a ventral typhlosole present in *C. californica* in the form of a muscular bulge (Figure 7, vt) between the openings of the style sac and the intestine, but it does not extend into the intestine. However, in the style sac the specialized cells along the right side of the ventral groove appear to be a remnant of the ventral typhlosole (Figure 8, vse). The dorsal typhlosole is not evident in the stomach of *C. californica*; however, it appears that the specialized cells along the left side of the ventral groove in the style sac may be remnants of the dorsal typhlosole (dse).

The cells lining the remainder of the style sac are heavily ciliated cuboidal epithelium (se), just as in *Batillaria zonalis*.

The arrangement of a separate style sac containing a ventral groove is not unique. GRAHAM (1939) described a similar situation in *Rissoa parva*, family Rissoacea. SESHAIYA (1929a) described a style sac groove in the species *Paludomus tranchaurica*; in the genera *Melanoides*, *Mysorella* and *Amnicola* (SESHAIYA, 1929b); and in the species *Potamides cingulatus*, family Cerithiidae (SESHAIYA, 1932).

The style is crystalline and proteinaceous in nature (BRIGHT, 1958). In 5 specimens the length of the style ranged from 14 to 16 mm and the height of the shell ranged from 28 to 30 mm. The ratio of style length to shell height was 0.51. The style normally extends the length of the style sac and into the stomach, where it dissolves as it rotates against the gastric shield. Of 25 live dissections, 2 revealed unusual style positions. In one case, the style extended beyond the gastric shield to the base of the stomach; in the other case, the style did not touch the gastric shield at all. The style entered the stomach to the left of the large stomach ridge and extended over the openings to the ducts of the digestive diverticula terminating at the posterior end of the large ridge.

The crystalline style of *Cerithidea californica* is firm, but flexible and does not dissolve in sea water, 70% isopropyl alcohol or Bouin's fixative.

In the stomach of *Cerithidea californica* the intestinal opening (Figure 7, ino) is to the left of the style sac opening. Several ciliated tracts lead to the intestinal opening along the stomach walls as in *Batillaria zonalis*.

Digestive Diverticula:

The opening to the duct of the digestive diverticula in *Batillaria zonalis* (Figure 5, odd) leads into a single main duct (Figure 2, vdd), which extends to the tip of the visceral hump along the ventral side. The main duct is lined with non-ciliated columnar epithelium. From the main duct there are numerous smaller ducts leading into the digestive diverticula tissue. These secondary ducts split once or twice and lead to sinuses lined by 2 types of cells which are very similar to those described to be digestive and excretory in nature in *Bithynia tentaculata* (FRETTER & GRAHAM, 1962) and in *Struthiolaria papulosa* (MORTON, 1951). The excretory cells are characterized by the presence of what appear to be excretory spherules.

The digestive diverticula in *Cerithidea californica* are similar to those of *Batillaria zonalis* in having a single ventral main duct (Figure 2b, vdd), lined with ciliated columnar epithelium as described by BRIGHT (1958). Also, the digestive diverticula of *C. californica* have a branching duct system leading to the sinuses lined with the same types of cells as found in *B. zonalis*.

The presence of a single ventral main duct in the digestive diverticula is reported to be common by E. H. Smith (personal communication) although FRETTER & GRAHAM (1962) commented that in many prosobranchs a pair of ducts is frequently found.

Intestine:

The intestinal groove in *Batillaria zonalis* (Figure 5, ing) leads directly into the intestine. The intestine makes a loop and then extends anteriorly along the right side of the mantle cavity and ends just inside the mantle edge at the anus. The first third of the intestine is characterized by the presence of a ventral intestinal typhlosole (int), which is an anterior extension of the ventral typhlosole of the stomach and style sac regions. The middle third of the intestine lacks the typhlosole and is the region where fecal pellets are formed. The last third of the intestine has folded walls capable of expanding to hold several fecal pellets at one time. The intestine is lined with ciliated columnar epithelium and scattered mucous cells.

In the stomach of *Cerithidea californica*, the intestinal opening (Figure 7, ino) is to the left of the opening of the style sac. There is a longitudinal ventral typhlosole present in the first section of the intestine, as in *Batillaria zonalis*, but it does not connect with the ventral typhlo-

sole in the stomach. Present with the typhlosole are 5 longitudinal ridges. The fold and ridges end after the first loop of the intestine. The next region is characterized by its resemblance to a triangle when seen in cross section due to 3 thickenings in the intestinal wall. This is the pellet-molding region. MORTON (1951) described a similar triangular region in *Struthiolaria papulosa*, which has the same function. The posterior portion of the intestine is similar to that in *B. zonalis*. The intestine ends just inside the right edge of the mantle cavity at the anus. The entire intestine is lined with ciliated columnar epithelium as BRIGHT (1958) described.

FUNCTIONAL MORPHOLOGY

Buccal Complex:

Batillaria zonalis feeds by scraping a fluid mixture of mud and detritus into its mouth with a radula. The radula rasps continually while the animal is on a moist substratum. Animals were not observed feeding while on a dry substratum. The radula draws the food material under and against a chitinous jaw within the mouth which causes the aggregated food particles to be broken into smaller pieces. Posterior to the jaw, the food particles are picked up by ciliary currents in the dorsal lateral grooves. As the particles proceed toward the esophagus, mucus is added from a pair of small buccal mucous glands. The dorsal lateral grooves become a single dorsal food groove in the esophagus.

The radula in *Cerithidea californica* functions in the same manner as the radula in *Batillaria zonalis*. However, the substratum on which *C. californica* feeds is finer and more uniform than that of *B. zonalis*, and it was always moist, resulting in a more continuous feeding habit than that of *B. zonalis*. Food is carried past the jaw, mixed with mucus from the small buccal mucous glands and moved posteriorly by ciliary currents to the dorsal food groove of the esophagus.

Both, *Batillaria zonalis* and *Cerithidea californica*, have short radulae which appear to be correlated to the soft substratum on which the animals feed (FRETTER & GRAHAM, 1962). In addition, both species possess only one pair of mucous secreting glands in the buccal complex. These glands are small, apparently because the food mixture is quite fluid and therefore mucus is only needed to bind the food into a food string and not needed to lubricate the radula. The probability that the mucus contains digestive enzymes is small. GRAHAM (1939) stated that since proteolytic enzymes from the buccal mucous glands will interfere with the functioning of a crystalline style, the function of the glands is accordingly modified in

style-bearing prosobranchs. In addition, FRETTER & GRAHAM (1962) reported that few prosobranchs secrete digestive enzymes in the mucus from buccal mucous glands.

Ciliary currents constitute the major means for transporting food material in the alimentary system of both species and the dorsal lateral grooves in the buccal complex are the beginning of this ciliary transport system. The currents created by the ciliary beat in the grooves efficiently channel the food material away from the radula and toward the esophagus, thereby preventing the buccal cavity from becoming clogged.

The functional morphology of the buccal complex of *Mysorella costigera* (SESHAIYA, 1930) and *Struthiolaria papulosa* (MORTON, 1951) is quite similar to that of *Batillaria zonalis* and *Cerithidea californica*. *Mysorella costigera*, a freshwater hydrobid with a crystalline style, feeds on fine moist detrital material in India and *S. papulosa*, a marine style-bearing ciliary feeder in New Zealand, also ingests fine detrital material.

Esophagus:

In *Batillaria zonalis*, food enters the dorsal food groove of the esophagus from the two dorsal lateral grooves of the buccal cavity and is carried posteriorly by ciliary currents. Almost no food is found in the anterior non-ciliated ventral portion of the esophagus. Although glandular-like tissue is present in the ventral esophagus, its function is unknown. Throughout the length of the esophagus, mucus is added to the food mixture, creating a food string. Ciliary currents continue to transport the food string posteriorly through the esophagus to the stomach.

In *Cerithidea californica*, as in *Batillaria zonalis*, food in the esophagus is carried by ciliary currents almost exclusively in a dorsal food groove. Ventrally there is no glandular tissue, as was found in the ventral esophagus of *B. zonalis*. Unlike *B. zonalis*, the dorsal food groove of *C. californica* blends into a multifolded expanded region just posterior to the area of torsion. Glandular tissue is absent; however, mucus is added to the food in the expanded region. Ciliary currents continue to carry the food string posteriorly to the stomach.

These findings agree specifically with those of GRAHAM (1939) concerning the modification of esophageal glandular areas in style-bearing gastropods. Graham reported that the glandular areas were either suppressed (which is the case in *Batillaria zonalis*) or replaced by ciliated and mucous cells with the walls retaining their expanded and folded nature (which is the case in *Cerithidea californica*). Graham concluded that a style and a series of glandular esophageal structures are alternative mechanisms, mutually inconsistent, for helping in the digestion of food.

Stomach and Style Sac:

In *Batillaria zonalis*, food is carried into the stomach mid-ventrally from the esophagus. Once in the stomach, the movements of food are affected by ciliary beat (Figure 5), stomach morphology, rotation of the style, muscular activity of the stomach walls and internal fluid pressures. New techniques, such as the use of X-rays, need to be developed before the effect of muscular activity of the stomach wall and the internal fluid pressures can be studied, since it is impossible to study their functioning once the stomach has been dissected.

Ciliary currents on the ventral surface of the stomach carry the food posteriorly to the base of the stomach and then anteriorly to the gastric shield and rotating style. The stomach ridge (sr and lr) keeps the food string in the groove leading to the gastric shield.

The style, which is rotating clockwise (seen from a posterior view) against the gastric shield is slowly dissolving and apparently releasing digestive enzymes, one of which is probably amylase (YONGE, 1932). Tall, slender glandular cells along the edge of the typhlosole (Figure 6, sse) within the style sac produce the style material which then is added to the entire length of the style sac as it rotates. The style is rotated by a strong ciliary current within the style sac and at the same time pushed against the gastric shield by the constant addition of style material to its tapered surface. The style material dissolves because the hydrogen ion concentration of the stomach is higher than that of the style sac, causing a change in viscosity of the style material (YONGE, 1932). The food material is caught in the dissolving end of the style and moved clockwise with it. The enzymes from the style begin digestion of the food by breaking down the larger usable particles.

The food particles are swept away from the style by ciliary currents on the dorsal wall which flow parallel to, but in opposite direction of, the style's rotation. The dorsal wall of the stomach (Figure 5, sa) is composed of numerous closely set ridges which serve as a sorting area for the food material. Larger particles, which would include most of the unusable material, break loose from the mucus and food mixture and are swept into grooves of the sorting area and then transported directly to the intestinal groove (ing) and then to the intestine (in) by ciliary currents.

MORTON (1953) has suggested that the slit between the style sac and the intestinal groove is functionally important in providing for the possible retrieval of undigested food material leaving the stomach. In *Batillaria zonalis* the position of the typhlosoles and the ciliary current on the surface of the ventral typhlosole functionally block communication between the intestine and the style

sac. There appears to be no retrieval mechanism in the stomach and style sac region of *B. zonalis*.

The smaller particles remain in the lumen of the stomach where the enzymes from the style continue to act on them. Multidirectional ciliary currents on the surface of the large ridge keep the stomach contents in motion. Periodically, muscular contractions of the stomach force food material into the digestive diverticula (odd), where digestion and absorption take place. As the stomach wall relaxes, the food mixture is drawn out of the digestive diverticula and picked up by ciliary currents on the floor of the stomach and carried anteriorly to the intestinal groove.

In *Cerithidea californica* food material enters the stomach mid-ventrally (Figure 7). It is prevented from being carried directly into the intestinal opening by a small ridge (sr_1). This feature is absent in *Batillaria zonalis*. The material is carried toward the gastric shield and rotating style by ciliary currents on the ventral wall of the stomach groove. The groove is bounded medially by 2 stomach ridges (sr_2 and lr), which is in contrast to the single stomach ridge in *B. zonalis*.

The style in *Cerithidea californica* rotates clockwise, slowly dissolving and releasing digestive enzymes as in *Batillaria zonalis*. Tall, slender glandular cells found along the ventral groove of the style sac of *C. californica* (Figure 8, vse and dse) secrete style material throughout the style sac, but primarily at the distal end. These glandular cells along the ventral groove are homologous to the glandular cells on the typhlosoles of the style sac in *B. zonalis*. This homology is supported by MORTON (1951), who has described the secretion of the style in *Struthiolaria papulosa* as coming from a narrow strip of tall cells along the typhlosole. The drawings of KUBOMURA (1957) diagramming cross sections of style sacs of the tectibranch *Philine japonica*, and the mesogastropod *Oncomelania nosophora*, show an area on the typhlosole of small, slender cells similar to those in both *B. zonalis* and *C. californica*. SESHAIYA (1930) found tall, slender cells along the typhlosole of the freshwater, style-bearing gastropod, *Mysorella costigera*, but did not discuss their function. Also, FRETTER & GRAHAM (1962) stated that most of the style substance is derived from the gland cells on the typhlosole.

Food material is swept away from the rotating style by currents on the dorsal wall of the stomach (Figure 7, sa). The dorsal wall acts as a sorting area and larger particles are moved into the grooves of the sorting area and are transported by ciliary currents into the opening to the intestine. The smaller particles remain in the lumen of the stomach where the digestive action continues and where ciliary currents and muscular contractions can move them into the duct to the digestive diverticula. In

contrast to *Batillaria zonalis*, in the stomach of *Cerithidea californica* a ciliated ventral groove (vg) is present between the two ventral ridges (lr and sr_2) which allows some of the food particles to re-enter the channel leading to the gastric shield and hence be re-sorted and digested further.

Material leaving the digestive diverticula is carried by ciliary currents toward the intestine channeled by a small ridge (sr_2) which prevents mixing of the material entering and leaving the stomach.

The basic functional morphology of the stomach and style regions of both, *Batillaria zonalis* and *Cerithidea californica*, are similar to most style-bearing mesogastropods. However, as YONGE (1932), GRAHAM (1939), and MORTON (1953) have stated, the stomach in style-bearers is the region most highly specialized for sorting and digesting a continuous stream of fine detrital material. In light of the apparent differences in substratum, and hence in ingested food in the species in this study, it is relevant to examine the detailed functional morphology of the stomach regions for possible correlations with food type.

As noted above, the food material ingested by *Cerithidea californica* is very fine and is composed of over 80% organic material. The ridges (sr_1 and sr_2) present in the stomach of *C. californica* are specialized structures which channel food material toward the areas of sorting and digestion. The first ridge (sr_1) prevents the incoming food material from becoming immediately mixed with the outgoing material and thus lost for digestive purposes. The second ridge (sr_2) serves to channel food material which has already passed over the dorsal sorting area back into the groove leading to the gastric shield and style where additional digestive material may be added to the mixture.

In contrast, in *Batillaria zonalis*, the food material ingested is poorly sorted and is low in organic content and the stomach morphology is less complex. Food material is moved through the stomach as a vaguely defined mass with few channeling ridges and with no recycling currents. The food material does not warrant specialized morphological features to prevent premature loss of food material nor does it need recycling to add further style enzymes for complete digestion.

This study suggests a relationship between style length and the composition of the ingested food. A general correlation between food type and functional morphology is well established. MACKINTOSH (1925) postulated that the presence of a style in gastropods may be correlated with the ingestion of diatoms and similar micro-organisms. YONGE (1930) stated that the presence of a style in gastropods is correlated with either a ciliary or a rasping mode of feeding and formulated the rule that the presence of a style means the animal is a specialized herbivore. YONGE

(1932) examined this correlation further and noted that while the style is restricted to herbivorous gastropods, it is not true that all herbivorous gastropods possess a style. Only those which supply finely divided food continuously to the stomach possess a style. GRAHAM (1939) stated that the style developed in those animals which feed continually on unicellular or small multicellular algae.

MORTON (1953) stated that the crystalline style sac in the Lamellibranchia remains generally longer and more specialized than in the Gastropoda. In the Lamellibranchia the gills sort the food material and reject the larger and heavier particles in "pseudofeces" before they enter the mouth. In comparison, *Cerithidea californica* feeds on a substratum which is already quite well sorted and highly organic in composition and correspondingly it possesses a relatively long style. In contrast, *Batillaria zonalis* with a short style, feeds on a substratum which is not as well sorted and which has a low organic content.

An enzyme supply sufficient to fully digest the available food would be advantageous for a slow, continuously feeding mollusk. It may be possible that an increase in available enzymes is brought about in those Lamellibranchia and Gastropoda which digest well sorted and highly organic food material through elongation of the style sac with a corresponding increase in style secreting tissue and style length. Assuming a fairly similar even rate of style production from species to species, the increase in style length would provide an increase in the supply of digestive enzymes.

Digestive Diverticula:

In *Batillaria zonalis* particles entering the digestive diverticula are well mixed with style mucus. This mixture is pumped down the main duct of the digestive diverticula (Figure 2a, vdd) by contractions of the stomach. No ciliary currents were observed to aid food movement in the main duct. Following each contraction the stomach relaxes and the material in the duct moves toward the stomach. These movements in the duct were observed only in intact specimens. The material in the secondary ducts moves in and out in an irregular manner which is independent of the movement in the main duct and indicates that the stomach contractions do not move material into the secondary ducts. Since there are no muscles in the digestive diverticula tissue, it appears that regulated ciliary currents may be responsible for movement in the secondary ducts.

In *Cerithidea californica* material is pumped in and out of the main duct of the digestive diverticula (Figure 2b, vdd), as in *Batillaria zonalis*, by stomach contractions. Also, material appears to enter and leave the secondary ducts by ciliary means as in *B. zonalis*. In *C. californica*,

however, there is a definite rhythm and timing to the movement within the secondary ducts which is independent of the movement of the main duct.

In both, *Batillaria zonalis* and *Cerithidea californica*, the movement of material through the branching system of the digestive diverticula first by muscular contractions and then by ciliary beat, functions to steadily bring the food material into contact with the digestive epithelium where intra-cellular digestion apparently takes place. The excretory spherules present in the epithelium, described previously, appear to be carried out of the tubules into the main duct of the digestive diverticula and from there into the ciliary currents on the ventral surface of the stomach which enter the intestine. The functioning of the digestive diverticula in both *B. zonalis* and *C. californica* appears very similar to that described by MORTON (1951) in *Struthiolaria papulosa*.

Intestine:

In *Batillaria zonalis*, after leaving the stomach, undigested and undigestible material enters the intestine where it is carried posteriorly by ciliary currents. The intestine appears to function solely to compact the food material into fecal pellets. HYMAN (1967) stated that the hydrogen ion concentration in the intestine is higher than it is in the stomach. This results in an increase in the viscosity of the intestinal mucus which serves to bind the fecal matter. The function of the ventral typhlosole in the anterior third of the intestine of *B. zonalis* is unclear. The mid-portion of the intestine molds the fecal matter into fecal pellets through the peristaltic action of the muscles lining the intestine. In the posterior portion the final mucous coating is added to the fecal pellets and the expanded region just anterior to the anus allows room for the pellets to be stored briefly while the mucous coating hardens. The fecal pellets are expelled periodically by peristaltic action and ciliary currents carry them away from the mouth along the right side of the foot and head.

In *Cerithidea californica* the intestine also appears to function solely for compacting and transporting the fecal matter out of the body cavity. The viscous intestinal mucus binds the fecal matter as in *Batillaria zonalis*. The ventral typhlosole in *C. californica* appears to function somewhat as a channel for the fecal material since the majority of the fecal matter was observed massed along the left side of the typhlosole. In addition, the 5 ridges present in *C. californica* may be specialized mucous secreting areas since the ridge tissue appears glandular in nature. The fecal material is molded into pellets in the mid-intestine and the mucous coating hardens in the expanded posterior region as in *B. zonalis*. The pellets are expelled and car-

ried away from the mouth in the same manner as in *B. zonalis*.

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